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Traits related to biological invasion: A note on the applicability of risk assessment tools across taxa

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Abstract

Biological invasions are occurring frequently and with great impact to agricultural production and other ecosystem services. In response to this, the Australian Weed Risk Assessment (AWRA) was created to assess the potential 'weediness' of plants based on answers to questions related to biogeography, undesirable attributes, and biology or ecology. This basic model has been expanded and adapted for use on other taxa, often without adequate validation. Since invasive insect crop pests are a major economic cost to agricultural production, there is interest in using an expanded model for insects. Here, we review traits related to invasiveness of insects based on a systematic review of the literature. We then compare the identified invasive traits of insects with those identified for plants in the AWRA. Using insects as a case study, we illustrate that although there is some overlap in invasive traits, there are many unique traits related to invasion for both insects and plants. For insects, these traits relate largely to social behaviour. This lack of congruence may also be the case for other taxa. To increase predictive power, a taxon-specific risk assessment tool and deliberate verification are required.

Keywords

Australian weed risk assessment, invasion traits, life history traits, risk assessment, systematic review, invasive insects

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Introduction

It is now widely accepted that invasive species are a major cause of global biodiversity loss, and as such, public interest in the topic has increased over recent decades (Didham et al. 2005). By way of increased transportation and international trade, biological invasions are occurring more frequently with increasingly undesirable costs to ecosystem services (Mack et al. 2000, Colautti et al. 2006). Although invasive species are defined in a number of ways with a variety of terms (Lockwood et al. 2013), often they are associated with 'harm' to the newly invaded environment (Mack et al. 2000). Because this is not always the case, and harm can be defined in many ways (Sagoff 2009), we follow Richardson et al. (2000b) and define 'invasive species' as those that have established and spread in a new geographic range.

In the United States alone, it has been estimated that 50 000 non-native species have been introduced, 4 500 of those being arthropods (Pimentel et al. 2005). Narrowed further, about 500 (11%) introduced insect and mite crop pest species have invaded (Pimentel et al. 2005), and the most economically important species of all agricultural pests are non-native (Mack et al. 2000). Approximately 95% of these arthropod introductions are accidental through entrance on plants, soil, ship ballast water, food sources, wood, etc (Pimentel et al. 2005, Rabitsch 2010). These crop pest introductions are estimated to cause US$13.5 billion dollars in damage annually in the United States due to crop loss and additional pesticide use (Pimentel et al. 2005). Economic impacts can also be indirect through restrictions on trade flow and market access changes (Roques et al. 2010). In comparison to the United States, 383 introduced insect species have been documented in the Czech Republic, of which 111 (29%) are considered either greenhouse or storage pests causing economic damage (Sefrova 2014). For just 10 nuisance invasive species (not just insect pests) in Canada, it was estimated that fisheries, forestry, and agriculture suffer a CDN$187 million loss annually (Colautti et al. 2006). In Europe, 1383 alien insects have been introduced and established to date, while the rate of introduction continues to accelerate (Roques et al. 2010). Despite substantial variation, species invasion is a global problem affecting a range of economically important services.

Government regulatory bodies have a legal responsibility to assess the risks of potential biotic invasions that could result in a detriment to plant resources, as dictated by the International Plant Protection Convention treaty (IPPC 1997). Thus, predictive pest risk assessment schemes have been created to assess invasion risks posed by plant species (e.g., Reichard and Hamilton 1997, Pheloung et al. 1999) based on the idea that certain life history traits increase the probability of invasiveness (Baker 1974). Using such schemes, plant species are evaluated for invasion risk according to the number and type of invasive traits they possess. For example, Reichard and Hamilton (1997) created a scheme to predict the invasion of woody plants in North America, yielding ~80% predictive success rate using life history and biogeographical attributes of a plant to predict invasion. In particular, reproductive attributes of the invader were important in predicting the invasive potential of woody plants (Reichard and Hamilton 1997).

Pheloung et al. (1999) expanded the decision tree method employed by Reichard and Hamilton (1997) to produce a computer-based spreadsheet checklist for invasive plants called the Australian Weed Risk Assessment (AWRA). The AWRA comprises 49 equally weighted questions, with sections on biogeography, undesirable attributes, and biology and ecology. The answers to these questions result in a score that informs the user about the potential 'weediness' of the plant, and from there a regulatory decision can be made. Pheloung et al. (1999) conclude that the AWRA can serve as a biosecurity tool to identify potentially invasive weeds, and can be modified for use in other locations. Currently the AWRA is used by the Department of Agriculture in Australia as a component of their multi-tiered WRA process (Department of Agriculture and Water Resources 2015). A comparison of the AWRA and other models (such as Reichard and Hamilton [2007]) found the AWRA to be the most accurate (Jefferson et al. 2004). The AWRA has since been modified and tested for invasive plants in New Zealand (Pheloung et al. 1999), the Hawaiian Islands (Daehler and Carino 2000), other Pacific islands (Daehler et al. 2004), Japan (Kato et al. 2006), the Czech Republic, and Florida (Gordon et al. 2008), with fairly consistent results. However, when the AWRA was tested for invasive plants in Canada, it was found to reject a high proportion of non-weedy species (McClay et al. 2010). Since Canada is characterized by cool, short growing seasons, simple alterations to the system that take cold-hardiness into account could increase the predictive power of the AWRA in Canada (McClay et al. 2010). Therefore, this system is generally accepted to function as a template for weed risk assessments across tropical and temperate geographies (Gordon et al. 2008).

Following the success of the AWRA, attempts have been made to create similar models for use with other taxa. Some models have evaluated potential invasive traits based on *a priori* hypothesized characteristics. For example, Causton et al. (2006) proposed a simple scoring system for identifying insects that are potentially invasive to the Galapagos Islands. However, it is not clear why Causton et al. (2006) chose the traits that they did, as the selection does not appear to be based on any systematic analysis. Similarly, Kolar and Lodge (2002) and Marchetti et al. (2004) do not provide reasoning for their selection of traits that were considered in their models for fish invasion. Additionally, the AWRA has been used as a basis for risk assessment schemes that are generalized for other non-native taxa (Table 1). Although this method might be useful because of its generality, it may not be valid if traits that are relevant to weediness in plants are not applicable to invasiveness in other taxa; its applicability remains unknown because the traits assessed in the AWRA have not been tested for relevance in other taxa.

The issue of transferability of invasive traits across taxa was investigated by Hayes and Barry (2008), who tested the significance of 115 invasive characteristics across seven taxonomic groups. Of the 49 studies included in their systematic review of predictors of invasion success, only two pertained to insects. Although they found some consistency in trait differences between native and invasive species, this was mainly only for plants. Overall, climate or habitat match was the only trait related to invasiveness *across* biological groups (Hayes and Barry 2008). Therefore, it is unclear whether a

Table 1. Examples detailing when the AWRA has been adapted for use on taxa other than plants.

Risk assessment model	Taxon	Reference
UK risk assessment scheme	Freshwater fish, marine fish, marine invertebrates, amphibian	Baker et al. 2008
FISK	Freshwater fish	Copp et al. 2005, Copp et al. 2008
MFISK	Marine fish	Copp et al. 2008
FI-ISK	Freshwater invertebrates	Copp et al. 2008
MI-ISK	Marine invertebrates	Coop et al. 2008
AmphISK	Amphibians	Copp et al. 2008
Infectious Agent Risk Assessment Module	Infectious agents	Copp et al. 2008
Generic Pre-screening Module	All other taxa	Copp et al. 2008

scheme created for use on plants can be generalized for use with other taxa. Traits that are related to invasiveness in plants may not generalize to other taxa, and if they do, their importance may not be similar across taxa.

Currently, there is no adequately validated, trait-based approach to risk assessment for insects, as there is for plants. Additionally, it remains unclear whether traits that are related to invasiveness in plants are generalizable to other taxa. Formal analyses are needed to determine traits predictive of invasiveness in taxa other than plants to ascertain the validity and generality of using a single risk assessment scheme across taxa. Because the AWRA has been expanded for use on other taxa, without validation, the aim of this paper is to compare questions in the AWRA with traits in the literature that are claimed to be related to insect invasion success.

As a first step in evaluating the generalizability of an invasion risk assessment scheme, we performed a systematic review of the literature for traits that are claimed to affect invasiveness in any insects. We compare these traits with those that are used to assess weediness in plants, and then discuss the potential validity of, and problems with, generalizing the AWRA for assessing the invasion risk of insects. We include all types of insects to gather the most trait data possible. This review, synthesis, and comparison of information is an important precursor to a larger project that will evaluate predictive traits and critical pathways of insect invasion with the overall objective of producing a comprehensive insect pest risk assessment scheme.

Methods

To determine whether there is congruence between traits related to invasion success in both plants and insects, we conducted a literature search that was completed in August 2015 using the Web of Science database (Thomson Reuters, New York, USA) and the following Boolean search adapted from Hayes and Barry (2008) in the "topic" function: (attributes OR correlates OR characteristics) AND (alien OR non-native OR non-indigenous OR exotic OR invasive) AND (invasion OR establishment) AND

(success OR predict) AND (insect OR invertebrate). The search resulted in approximately 3 500 results; from this, 125 articles were identified as relevant (i.e. they minimally discussed a biological or environmental trait of an invasive insect) by examining the article abstract. Papers were included in our analysis if they tested or claimed traits that were related to invasion success in insects (i.e. other classes of invertebrates were excluded). Papers that were included were then screened for experimental, observational, or anecdotal information pertaining to traits of invasive or native insects. These data were extracted and compiled into a spreadsheet to highlight whether differences existed between invasive and native insects, and between invasive plants and invasive insects. The data we included were: the trait being tested or claimed, the trait type (life history or environmental), the trait states (invasive vs. native), the reference, and what the significance or application of this result was.

Results and discussion

We identified a total of 79 traits that were claimed to have some relation to invasiveness in insects (Table 2). We grouped the most similar traits together to avoid repetition, and we assigned categorical nomenclature (Table 3 and 4). Traits that related to the same life processes were assigned to the same group. For example, the trait *dispersal* includes flight speed, flight distance, flight temperature, dispersal type, dispersal habitat, and colonization ability. Consolidation of similar traits resulted in a total of 29 trait groups that are allegedly related to invasion success in insects. These 29 trait groups were divided into life history (Table 3) and environmental traits (Table 4) and compared against plant traits used to assess weediness in the AWRA to determine if there are clear analogues between insect and plant invasiveness traits.

For insect invasion-related traits, it is noteworthy that some of the evidence is contradictory, i.e., a positive relation with invasiveness in some cases and a negative relation in others, and universal statements may not be accurate. For example, *body size* can either be positively or negatively associated with invasion (Table 2). It is self-evidently problematic to include contradictory traits in a risk assessment scheme based on universal statements.

Analogous insect and plant invasiveness traits

We identified 18 of 29 claimed invasive trait groups for insects that were represented by clear analogues of weedy traits in plants (Tables 1 and 2). This might lend some validity to a generalization of the AWRA for use on insects. However, whether these analogous traits infer invasiveness in insects in the same way, or to the same degree, as they do in plants has yet to be formally tested. By using decision tree modelling or similar methods to identify traits that are most important to invasion of insects, it would be possible to assess whether these traits hold similar ranks of importance

Table 2. Life history and environmental traits related to invasion, highlighting the suggested differences between invasive and native insects that were found through an extensive literature review.

Insect trait	Trait component	Differences between invasive and non-invasive insects	Type of evidence†
Life history traits			
Feeding guild	Feeding niche	Invasive insects predominantly sap feeders and detritivores (Kenis et al. 2007)	C
	Feeding guild	Herbivores more likely to establish than predators and parasitoids (Engelkes and Mills 2011); Parasitoids more likely to establish than predators (Kimberling 2004)	A, C
	Taxon	Diptera and Lepidoptera fastest to disperse, Coleoptera slowest (Paynter and Bellgard 2011) Invasive species predominantly Hemiptera (56.4 %), Lepidoptera (14.9 %), and Hymenoptera (12.9 %) (Matosevic and Zivkovic 2013); Invasive species predominantly Homoptera (39 %), Coleoptera (19 %), Lepidoptera (13 %), and Hymentoptera (13 %) (Mattson et al. 2007); Invasive species predominantly Coleoptera, Sternorrhyncha, and Psocoptera (Kenis et al. 2007); Homoptera and Lepidoptera most likely to establish (Peacock and Worner 2008)	C
	Feeding method	Miners, borers, and leaf-rollers disperse faster than external feeders, and root-, rosette-, and seed-feeders (Paynter and Bellgard 2011) Internal feeders more likely to establish than external feeders (Kimberling 2004) Insects that use single host species are more likely to establish than those that use multiple hosts (Mondor et al. 2007)	C
Diet breadth	Diet breadth or Host specificity	Invasive insects have a wide diet breadth (generalist) compared to natives (Moller 1996, Cervo et al. 2000, Kasper et al. 2004, Kimberling 2004, Moeser and Vidal 2005, Snyder and Evans 2006, Mondor et al. 2006, Ward and Masters 2007, Wilson et al. 2009, Orledge et al. 2010, Andersen et al. 2011)	A, C, E, O
Generation onset	Voltinism (number of generations per year)	Dispersal rate increases as number of generations/year increases (Yan et al. 2005, Paynter and Bellgard 2011); Insects with multiple generations per year more likely to establish than insects with one generation per year (Kimberling 2004)	A, C
	Adult emergence	Invasive insects emerge earlier than natives (Hack and Lawrence 1995, Pickett and Wenzel 2000, Gamboa et al. 2002, Gamboa et al. 2004, Boivin et al. 2008)	A, E, O
	Onset of egg laying	Invasive insects start laying eggs earlier than natives (Kajita and Evans 2010b, Laugier et al. 2013)	E, O
Development	Growth rate	Invasive insects have rapid growth rates compared to natives (Labrie et al. 2006, Ward and Masters 2007)	A, O
	Preimaginal (pre-adult) development time	Invasive insects have shorter preimaginal development time than natives (Cervo et al. 2000, Gamboa et al. 2004, Boman et al. 2008, Delatte et al. 2009); Invasive insects have a longer preimaginal development time than natives (Bonato et al. 2007)	A, E, O

Insect trait	Trait component	Differences between invasive and non-invasive insects	Type of evidence†
	Generation time	Invasive insects have shorter generation time than natives (Facon et al. 2011); Short generation times increase colonization success (Yan et al. 2005)	A, E
	Intrinsic rate of increase	Invasive insects have higher intrinsic rate of increase than natives (Crawley 1987, Duyck et al. 2007, Delatte et al. 2009, Orledge et al. 2010)	A, C, E, O
	Intrinsic death rate	Invasive insects have lower intrinsic death rate than natives (Duyck et al. 2007, Foucaud et al. 2013)	A, E, O
Dispersal	Flight speed	Invasive insects have higher flight speeds than natives (Sun et al. 2013); Flight speed can enhance invasion (Lombaert et al. 2014)	A, E, O
	Flight distance	Invasive insects can fly longer distances than natives (Yan et al. 2005)	A
	Flight temperature	Invasive insects can fly within a broader range of temperatures than natives (Yan et al. 2005)	A
	Dispersal type	Insects capable of flight more likely to disperse than wind-dispersed or crawling species (Moller 1996, Paynter and Bellgard 2011); Macropterous individuals increases dispersal ability (Niemelä and Spence 1991)	A, C, O
	Dispersal habitat	Aquatic insects disperse faster than terrestrial insects (Paynter and Bellgard 2011); Permanent stream flow enhances invasion (Holway 1998)	C, O
	Colonization ability	Invasive insects have better colonization ability than natives (Harcourt et al. 1998, Yan et al. 2005)	A, O
Desiccation resistance	Desiccation resistance	Invasive insects more resistant to desiccation than natives (Parkash et al. 2014)	E, O
Mating behaviour	Copulatory behaviour	Invasive insects faster to copulate than natives (Laugier et al. 2013); Female invasive insects fertilized by more males than native females (Laugier et al. 2013); Invasive insects copulate more effectively than natives (Liu et al. 2007, Crowder et al. 2010)	A, E
Thermal resistance	Temperature tolerance	Invasive insects have lower temperature tolerance than natives (Wuellner and Saunder 2003, Bonato et al. 2007, Peacock and Worner 2008, Delatte et al. 2009, McGrannachan and Lester 2013, Parkash et al. 2014); Invasive insects have higher temperature tolerance than natives (Michaud 2002, Wuellner and Saunder 2003, Bonato et al. 2007, Delatte et al. 2009, Ju et al. 2013) Invasive insects have a higher lower developmental threshold than native insects (Jarošík et al. 2015)	C, E, O
Overwintering behaviour	Aggregate overwintering	Invasive insects overwinter in aggregate, whereas natives do not (Cottrell and Shapiro-Ilan 2003)	E, O
	Overwintering site	Invasive insects overwinter in sheltered habitat, whereas natives do not (Yan et al. 2005)	A
	Winter survival	Invasive insects have higher winter survival than natives (Inoue 2011, Raak-van den Berg et al. 2012)	E, O

Insect trait	Trait component	Differences between invasive and non-invasive insects	Type of evidence†
Body size	Body size	Invasive insects are smaller than natives (Crawley 1987, McGlynn 1999b, Gamboa et al. 2004, Ness et al. 2004, Cremer et al. 2006, Mondor et al. 2006, Cremer et al. 2008, Wilson-Rich and Starks 2010, Abril et al. 2013); Small insects more likely to establish than large insects (Lawton et al. 1986, Lester 2005); Invasive insects are larger than natives (Ings et al. 2006, Delatte et al. 2009, Kajita and Evans 2010a, Kajita and Evans 2010b); Large body size may promote invasion success (Moller 1996)	A, C, E, O
	Offspring mass	Invasive insect offspring mass smaller than native offspring mass (Armstrong and Stamp 2003)	E
Functional group	Functional group	Invasive insects predominantly cryptic, generalized Myrmicinae, and opportunists (McGlynn 1999a)	C
Fecundity characters	Lifetime performance	Invasive insects have higher lifetime performance (product of hatching rate, larval survival, and subsequent fecundity) than natives (Facon et al. 2011); High progeny production increases colonization success (Yan et al. 2005)	A, E
	Egg laying behaviour	Insects that lay eggs in batches less likely to become invasive (Crawley 1987)	
	Egg size	Invasive insects lay larger eggs than natives (Duyck et al. 2007, Delatte et al. 2009); Invasive insects lay smaller eggs than natives (Kajita and Evans 2010a)	A, E, O
	Fecundity	Invasive insects are fecund later than natives (Armstrong and Stamp 2003); Invasive insects allocate more resources to fecundity than natives (Curtis et al. 2005); Invasive insects have higher fecundity than natives (Pickett and Wenzel 2000, Michaud 2002, Duyck et al. 2007, Boivin et al. 2008, Delatte et al. 2009, Kajita and Evans 2010a, Kajita and Evans 2010b, Laugier et al. 2013); Invasive insects have higher net reproductive rate than natives (Duyck et al. 2007, Delatte et al. 2009); Invasive insects have higher gross reproductive rate than natives (Moller 1996, Duyck et al. 2007);	A, E, O
	Egg viability	Invasive insects have higher egg viability than natives (Michaud 2002)	E, O
	Juvenile survival	Invasive insects have higher juvenile survival than natives (Duyck et al. 2007, Delatte et al. 2009);	A, E, O
	Percentage paternity	Invasive insects have higher percentage paternity than natives (Laugier et al. 2013);	E
	Pupal mass	Invasive insect pupae are larger than natives (Duyck et al. 2007)	A, O
Competitive ability	Competitive ability, adaptive ability	Invasive insects can outcompete natives (Holway 1999, Thomson 2004, Snyder and Evans 2006, Rowles and O'Dowd 2007, De Barro and Bourne 2010, Wilson and Holway 2010, Sanders and Suarez 2011, Auger-Rozenberg and Roques 2012, Wilder et al. 2013); Interspecific competition may limit invasion (LeBrun et al. 2007); Invasive insects can use resources that natives cannot (Orledge et al. 2010); Invasive insects can use resources in their introduced range that they cannot in their native range (Yan et al. 2005, Sun et al. 2013); Invasive insects avoid predation through crypsis (Yan et al. 2005)	A, C, E, O

Insect trait	Trait component	Differences between invasive and non-invasive insects	Type of evidence†
	Predation	Invasive insects prey upon native insects (Wilson and Holway 2010)	E, O
Reproduction	Reproductive strategy	Invasive insects may be asexual, whereas natives reproduce sexually (Moller 1996, Mondor et al. 2006, Peccoud et al. 2008, Mikheyev et al. 2009, Caron et al. 2013)	A, C, E, O
Oviposition site	Oviposition site	Insects that oviposit internally more likely to establish than insects that oviposit outside of host (Kimberling 2004)	C
Sex ratio	Sex ratio	Invasive insects have female-skewed sex ratio, whereas natives do not (Michaud 2002, Liu et al. 2007)	E, O
Intraguild predation	Intraguild predation	Invasive insects are stronger intraguild predators than natives (Michaud 2002, Snyder et al. 2004, Roy et al. 2008a); Native insects consume more conspecific eggs than invasive insects (Michaud 2002); Invasive insects consume more heterospecific eggs than natives (Michaud 2002, Ware et al. 2009)	E, O
Foundress activity	Foundress activity	Invasive insect foundresses build and repair nests more often than natives (Armstrong and Stamp 2003); Invasive insect foundresses more aggressive towards offspring than natives (Armstrong and Stamp 2003)	E
Aggression	Level of aggression	Invasive insects show less intraspecific aggression compared to natives (Holway et al. 1998, Suarez et al. 1999, Le Breton et al. 2004, Errard et al. 2005, Cremer et al. 2008, Fournier et al. 2009, Perdereau et al. 2011, Sanders and Suarez 2011, Suhr et al. 2011, Ugelvig and Cremer 2012, Hoffmann 2014); Low intraspecific aggression may promote invasion success (Moller 1996); Invasive insects show more interspecific aggression than natives (Human and Gordon 1999, Cremer et al. 2006, Duyck et al. 2006, Snyder and Evans 2006, Rowles and O'Dowd 2007, Carpintero and Reyes-Lopez 2008, Fournier et al. 2009, Blight et al. 2010, Perdereau et al. 2011)	A, E, O
	Usurpation	Native insects attempt usurpation more often than invasive insects (Gamboa et al. 2002, Gamboa et al. 2004); Usurpation may increase establishment success (Moller 1996)	A, O
Colony characteristics	Colony productivity	Invasive insect nests (combs) contain more cells than natives (Pickett and Wenzel 2000, Gamboa et al. 2002, Gamboa et al. 2004); Colony budding may increase establishment success (Moller 1996, Tsusui and Suarez 2003) Invasive insects produce more adults than natives (Gamboa et al. 2004)	A, E, O
	Relatedness to queen	Invasive insects are less related to their queen than natives (Ross et al. 1996)	O
	Polygyne social form	Invasive insects are polygyne (multiple egg-laying queens per nest) (Yang et al. 2012)	O
	Unicoloniality	Invasive insects are unicolonial, whereas natives are multicolonial (Tsusui and Suarez 2003, Le Breton et al. 2004, Errard et al. 2005, Cremer et al. 2008, Suarez et al. 2008, Fournier et al. 2009, Wilson et al. 2009, Sanders and Suarez 2011, Ugelvig and Cremer 2012, Hoffmann 2014)	A, E, O
	Sociality	Social insects are likely to become invaders (Moller 1996)	A

Insect trait	Trait component	Differences between invasive and non-invasive insects	Type of evidence†
	Recognition cues	Invasive insects are more chemically similar than natives (Errard et al. 2005, Cremer et al. 2008, Brandt et al. 2009, Fournier et al. 2009, Perdereau et al. 2011); Invasive insects are more genetically similar than native insects (Tsusui and Suarez 2003, Suarez et al. 2008, Ugelvig and Cremer 2012)	A, E, O
	Colony longevity	Shift from small, annual colony to large, perennial colony can increase invasion success (Wilson et al. 2009)	E, O
Queen characteristics	Queen longevity	Queen longevity is greater in invasive insects than in natives (Gamboa et al. 2002)	O
	Queen number	Invasive insects have more queens per nest than natives (Ross et al. 1996, Tsusui and Suarez 2003, Abril et al. 2013); Invasive insects produce more gynes (reproductive female caste) than native insects (Pickett and Wenzel 2000, Ings et al. 2006)	A, E, O
Nesting	Nesting habitat	Ground nesting ants more likely to establish than arboreal ants (Suarez et al. 2005); Invasive insects nest in urban areas, whereas natives nest in rural areas (Downing 2012)	C, O
	Nest predation	Invasive insect nests suffer less predation than native nests (Cervo et al. 2000); Invasive insects more likely to re-nest after predation than natives (Gamboa et al. 2004)	A, O
	Nest reutilization	Invasive insects may reuse a nest, whereas natives seldom do (Cervo et al. 2000)	A
Environmental traits			
Natural enemies present	Presence of predators	Presence of predators decreases invasive insect abundance and increases native insect development rate (Juliano et al. 2010); Dispersal increases as presence of parasitoids in native range increases (Paynter and Bellgard 2011); Absence of predators/parasitoids increases the likelihood of establishment (Lawton et al. 1986, Tsusui and Suarez 2003, Yan et al. 2005, Snyder and Evans 2006, Suarez et al. 2008, Ugelvig and Cremer 2012)	A, C, E
	Rate of parasitism	Invasive insects parasitized less often than natives (Cervo et al. 2000, Gamboa et al. 2002, Gamboa et al. 2004, Allen et al. 2007, Cremer et al. 2008, Gray et al. 2008, Orledge et al. 2010, Comont et al. 2014); Invasive insects have higher parasite prevalence than natives (Jones and Brown 2014)	A, C, E, O
	Fungal susceptibility	Invasive insects less susceptible to fungal infections compared to natives (Cottrell and Shapiro-Ilan 2003)	E, O
	Immunocompetence	Invasive insects have a lower immune response than natives (Wilson-Rich and Starks 2010, Manfredini et al. 2013)	E, O
	Antimicrobial defence	Invasive insects have an efficient immune system (Vilcinskas et al. 2013)	E
Environmental matching	Host range	Invasive insects have wider host range than natives (Crawley 1987, Peacock and Worner 2008); Certain mutualistic interactions will enhance invasion success (Wilder et al. 2011); Presence of suitable host species increases invasion success (Brooks et al. 2012, Graziosi and Rieske 2012, Sun et al. 2013); Synchronization with host species increases invasion success (Harcourt et al. 1988); Phenological plasticity increases invasion success (Ward and Masters 2007)	A, C, E, O

Insect trait	Trait component	Differences between invasive and non-invasive insects	Type of evidence†
	Soil type	High-moisture soils promote insect invasion (Bolger 2007); Invasive insects more active at higher soil temperatures than natives (Human et al. 1998)	O
	Humidity	Invasive insects prefer high humidity, whereas natives do not (Walters and Mackay 2003); Invasive insects have more extreme high and low humidity tolerances than natives (Wuellner and Saunder 2003)	E, O
	Elevation	Invasive insects prefer low elevation, whereas natives prefer high elevation (Human et al. 1998, Arndt and Perner 2008, Fitzgerald and Gordon 2012)	O
	Climate matching	Invaded range must be climatically suitable for the invasive insect (Simberloff 1989, Holway 1998, Koch et al. 2006, Gray et al. 2008, Roura-Pascual et al. 2011, Sun et al. 2013)	A, C, E, O
	Light tolerance	Invasive insects have more extreme high and low light tolerances than natives (Wuellner and Saunder 2003)	O
	Habitat type	Invasive insects prefer dry cultivated fields over shrublands and plantations (Roura-Pascual et al. 2011); Invasive insects more abundant in cool, dry areas, whereas native insects are more abundant in warm, humid areas (Parkash et al. 2014); Invasive insects prefer open land, whereas natives prefer forests (Ishii et al. 2008); Invasive insects prefer agricultural lands (56.4 %), followed by parks and gardens (28.7 %), and woodlands and forests (14.9 %) (Matosevic and Zivkovic 2013)	C, E, O
Propagule pressure	Propagule pressure	Greater numbers of introduced propagules and greater numbers of introductions increase the probability of establishment (Beirne 1975, Simberloff 1989, Hopper et al. 1993, Hight et al. 1995, Memmott et al. 1998, Grevstad 1999, Memmott et al. 2005, Suarez et al. 2005, Walters and Mackay 2005, Ward and Masters 2007, Mikheyev et al. 2008, Tobin et al. 2013); Propagule size found not to affect establishment (Sagata and Lester 2009)	A, C, E, O
Disturbance	Environmental disturbance	Environmental disturbance decreases abundance of native species while increasing abundance of invasive species (Human et al. 1998, Zettler et al. 2004, Arndt and Perner 2008, Suarez et al. 2008, Fitzgerald and Gordon 2012); Environmental disturbance positively associated with invasion success (Simberloff 1989, Snyder and Evans 2006, Roura-Pascual et al. 2011); Environmental disturbance decreases the abundance of invasive species (Arndt and Perner 2008); Environmental disturbance negatively associated with invasion success (Yeates et al. 2012)	A, C, E, O
Resistance evolution	Resistance to insecticide	Invasive insect able to evolve resistance to insecticide, leading to exclusion of native insect (Crowder et al. 2010)	A, E
Biotic resistance	Biotic resistance	Insects able to invade due to lack of biotic resistance in the native assemblage (Niemelä and Spence 1991, Yan et al. 2005); Areas with high biotic resistance are less prone to invasion (Walters and Mackay 2005, Blight et al. 2010, Roura-Pascual et al. 2011)	A, C, E, O

Insect trait	Trait component	Differences between invasive and non-invasive insects	Type of evidence†
Foraging	Foraging rate	Foraging rate is greater in invasive insects than natives (Human and Gordon 1996, Holway et al. 1998, Gamboa et al. 2002, Ings et al. 2006, McGrannachan and Lester 2013)	E, O
	Predatory efficiency	Invasive insects more efficient at capturing prey than native insects (Labrie et al. 2006, Dejean et al. 2007); Invasive insects consume more prey than native insects (Labrie et al. 2006); Invasive insects are more efficient at exploiting resources than native insects (Sanders and Suarez 2011)	A, E, O
	Foraging distance	Invasive insects will travel farther than native insects to forage (Perdereau et al. 2011)	E, O
	Foraging behaviour	Invasive insects show flexible foraging behaviour (Wilson-Rankin 2014); Invasive insects forage throughout the year, whereas native insects do not forage during winter (Wuellner and Saunder 2003); Invasive insects start foraging earlier in the day than natives (Gamboa et al. 2004)	E, M, O
	Bait recruitment	Invasive insects recruit to bait faster than natives (Holway 1999, Dejean et al. 2007, Rowles and O'Dowd 2007, McGrannachan and Lester 2013); Invasive insects recruit to more bait types than natives (Human and Gordon 1996, Holway 1998, Holway 1999)	E, O

† A = Anecdotal information (no evidence given), C = correlational analysis (analyses using pre-existing data), E = experimental (standard experiment using treatments and controls), M = meta-analysis, O = observational (observational study with no experimental manipulation).

Table 3. A comparison of life history traits related to insect invasion and traits considered in the Australian weed risk assessment for plants.

Insect trait	Invasive trait measures	Plant equivalent
Feeding guild	Feeding guild, feeding site, feeding niche, taxon, lifestyle category	Parasitic, allelopathic
Diet breadth	Diet breadth, host specificity	Broad climatic suitability (environmental versatility)
Desiccation resistance	Desiccation resistance	Broad climatic suitability (environmental versatility)
Thermal resistance	Temperature tolerance	Broad climatic suitability (environmental versatility)
Overwintering behaviour	Winter survival, aggregate overwintering, overwintering site	Broad climatic suitability (environmental versatility)
Generation onset	Generations per year, adult emergence, onset of egg laying	Minimum generative time
Development	Preimaginal development time, growth rate, generation time, intrinsic rate of increase, intrinsic death rate	Minimum generative time
Dispersal	Dispersal type, dispersal habitat, colonization ability, flight speed, flight temperature, flight distance	Dispersal mechanisms
Body size	Body size, offspring mass	Seed size
Functional group	Functional group	Plant type
Mating behaviour	Copulatory behaviour	Reproduction
Fecundity	Fecundity, egg viability, Net Reproductive Rate (NRR), egg size, Gross Reproductive Rate (GRR), percentage paternity, juvenile survival, lifetime performance, egg laying behaviour, pupal mass	Reproduction
Reproduction	Reproductive strategy	Reproduction
Competitive ability	Competitive ability, adaptive ability, predation	Climbing or smothering growth habit
Oviposition site	Oviposition site	None
Sex ratio	Sex ratio	None
Intraguild predation	Intraguild predation	None
Foundress activity	Foundress activity	None
Aggression	Aggression, usurpation	None
Colony characteristics	Recongnition cues, sociality, queen relatedness, colony productivity, polygyne social form, unicoloniality, colony longevity	None
Queen characteristics	Queen number, queen longevity	None
Nesting	Nesting habitat, nest predation, nest reutilization	None
None	None	Species has weedy races

Insect trait	Invasive trait measures	Plant equivalent
None	None	Species has a congeneric weed
None	None	Produces spines, thorns, or burrs
None	None	Unpalatable to grazing animals
None	None	Toxic to animals
None	None	Causes allergies or is otherwise toxic to humans
None	None	Prolific seed production
None	None	Evidence that a persistent propagule bank is formed (>1 yr)

Table 4. A comparison of environmental traits related to insect invasion and traits considered in the Australian WRA for plants.

Insect trait	Invasive trait measures	Plant equivalent
Natural enemies present	Presence of predators, rate of parasitism, fungal susceptibility, antimicrobial defense, immunocompetence	Effective natural enemies present
Environmental matching	Host range, climate matching, soil type, humidity, elevation, light tolerance, habitat type	Species suited to climate, quality of climate match data, broad climatic suitability (environmental versatility)
Disturbance	Environmental disturbance	Broad climatic suitability (environmental versatility); tolerates or benefits from mutilation, cultivation, or fire
Propagule pressure	Propagule pressure	Dispersal mechanisms
Resistance evolution	Resistance to insecticide	None
Biotic resistance	Biotic resistance	None
Foraging	Foraging rate, foraging behaviour, predatory efficiency, foraging distance, bait recruitment	None
None	None	Species is highly domesticated
None	None	Species has become naturalized where grown
None	None	Native or naturalized in regions with extended dry periods
None	None	Species has a history of introductions outside its natural range
None	None	Species is naturalized beyond its native range
None	None	Garden/amenity/disturbance weed
None	None	Weed of agriculture/horticulture/forestry
None	None	Environmental weed
None	None	Creates a fire hazard to natural ecosystems
None	None	Is a shade tolerant plant at some stage in its life cycle
None	None	Grows on infertile soils
None	None	Forms dense thickets
None	None	Well controlled by herbicides

between plants and insects. Furthermore, certain insect trait groups can be measured through numerous proxies. For example, the insect *development* trait group comprises a number of measures related to development that are potentially indicative of invasion. In contrast, the AWRA has only one question related to plant development, called *minimum generative time*. The fact that more developmental characteristics were claimed to be related to invasion in insects does not necessarily mean that development is more important in the invasion success of insects than in plants. This discrepancy may mean that more questions could be developed relating to insect development in a modified pest risk assessment. Conversely, if the multiple insect development measures have similar reliability, the one that is easiest to measure (e.g., development time, rather than development plasticity) could be chosen for inclusion in the risk assessment. However, it is possible that some of these trait groups are more predictive than others, and as such, all else being equal, the measures that are most predictive should be included in a risk assessment if multiple traits are correlated. This same issue arises with other insect trait groups, particularly *generation onset*, *overwintering behaviour*, *fecundity characters*, *environmental matching*, *foraging*, and *colony characteristics*.

Unique invasiveness trait groups of insects

We identified 11 of 29 trait groups that seem to be uniquely related to insect invasion and have no clear analogue to plant traits. These trait groups involved both life history and the environment. This result suggests that a pest risk assessment developed for plant invasion may not be applicable for insects because traits that are important to insect invasion may be missing from the assessment. We next examine these unique insect life history and environmental trait groups in further detail.

Sex ratio: In sexually reproducing species, the intrinsic rate of population increase is generally limited by the number of females rather than the number of males. For example, *sex ratio*, specifically female dominance, can increase the successful establishment of biological control agents such as *Harmonia axyridis* (Asian lady beetle; Michaud 2002, Kimberling 2004). *Harmonia axyridis* has a female-skewed sex ratio that may give it intrinsic advantages over the native *Cycloneda sanguinea* (spotless lady beetle; Michaud 2002). A female-skewed sex ratio can compound the effect of high *per capita* fecundity, leading to explosive population growth, by which such invasive species may outcompete native species, or escape control by natural enemies. Aspects of plant reproduction are considered in the AWRA, such as self-fertilization and viable seed production, which may be distantly analogous to sex ratio in insects.

Oviposition site: According to Kimberling (2004), *oviposition site* can influence the establishment of alien insects whereby those who oviposit on or inside the host are more likely to establish. Although Kimberling does not discuss the reasoning for this association, we assume that larvae are not required to find a host upon hatching, so that individuals are more likely to achieve their developmental requirements. By contrast, eggs that are deposited elsewhere would be more susceptible to damage and

death before finding a suitable host, and individuals would be less likely to complete development. Although seed dispersal mechanisms are considered in the AWRA, *oviposition site* is not included because it is not relevant to plants.

Intraguild predation: Organisms that kill potential competitors within their feeding guild are referred to as intraguild predators. For example, the invasive *H. axyridis* is more likely than the native *Coccinella septempunctata* (seven-spot ladybird) to consume the cadavers of *Pandora neoaphidis* fungus-infected aphids (Roy et al. 2008a), a form of intraguild predation. Although study of other members of the aphidophagous and coccidophagous guilds is lacking, evidence indicates that *H. axyridis* may affect the population of *P. neoaphidis* more negatively than would *C. septempunctata*, leading to a greater competitive advantage for *H. axyridis*. In addition, *H. axyridis* will consume more heterospecific eggs (i.e., *Adalia bipunctata* eggs) than the native *A. bipunctata* will consume *H. axyridis* eggs (Ware et al. 2009). This also indicates a competitive advantage for the invasive insect over the native.

Resistance evolution: Because insecticides are commonly used to control invasive insects, the evolution of pesticide resistance would benefit species that are capable of evolving rapidly (Crowder et al. 2010). This trait has been recognized in the invasive biotype of the cryptic *Bemisa tabaci* (whitefly) species complex, which was able to displace other whiteflies competitively through adaptation to an insecticide (Crowder et al. 2010). The AWRA does not explicitly consider whether a plant is able to evolve resistance to herbicides; however, the trait *well controlled by herbicides* is included as a persistence attribute. Although it is possible that a plant will evolve resistance to an herbicide, a plant may resist control by an herbicide due to the specific mode of action; therefore, although these two traits may seem similar (*resistance evolution* and *well controlled by herbicides*), we consider them as different.

Biotic resistance: Native species richness can affect the extent to which biological invasions are likely to occur such that environments with greater species richness are often less easily invaded (Byers and Noonburg 2003). Although this may be a scale-dependent effect with multiple contributing factors such as disturbance, propagule pressure, and environmental stress (Byers and Noonburg 2003), environments with high *biotic resistance* by native fauna (i.e. areas with an abundance of similar species or containing competitors and predators) may provide protection against foreign invaders. For example, certain native ant species provide biotic resistance against the invasion of *Linepithema humile* (Argentine ant; Blight et al. 2010, Roura-Pascuala et al. 2011). Although there is evidence for biotic resistance against invading plants (Maron and Vila 2001), it is possible that this trait is not included in the AWRA because it could be a difficult parameter to measure. *Biotic resistance* may also be correlated to plant invasion through other explicit traits and therefore not warranted for inclusion in the AWRA. For example, at large scales, native and exotic plant diversity are positively related because they are driven by factors related to spatial heterogeneity (e.g. differences in soil measures such as soil depth and nitrogen; Davies et al. 2005).

Foraging: There is considerable diversity in the foraging abilities and behaviours of insects that affect their invasive potential. The *foraging* trait group includes the traits:

search efficiency, *foraging rate*, *bait recruitment*, *foraging behaviour*, *predatory efficiency*, and *foraging distance* (Table 2). For example, invasive ants are able to dominate native communities with respect to the rate and efficiency with which they forage, which may alter the food web structure in their favour (Human and Gordon 1996, Holway 1998, Holway 1999, Gamboa et al. 2002, Ings et al. 2006, Dejean et al. 2007, Rowles and O'Dowd 2007, McGrannachan and Lester 2013). Invasive ants have been found to forage at times of the year when native ants do not (Wuellner and Saunder 2003), and invasive wasps exhibit flexible foraging behaviour (Wilson-Rankin 2014). Overall, these traits imply dominance over the native community with respect to resource acquisition and may be important in invasion success. Although plants do not actively forage or recruit to bait, the AWRA does consider whether a plant is able to grow on infertile soils or fix nitrogen; these characteristics relate to the ability of the plant to acquire water and nutrients from the soil, which is related to but different from *foraging* behaviour in insects (but see e.g. Sutherland and Stillman 1988 for an alternative perspective).

Colony characteristics: Invasive ants (Holway et al. 2002), bees (Goulson et al. 2003), and wasps (Beggs et al. 2011) are some of the most widely studied invasive insects, and thus, many characteristics of social insect colonies are claimed to affect invasion potential. Traits included in this category are: greater *colony productivity* and *longevity*, decreased *relatedness to queen*, *polygyne social form*, *sociality*, *unicoloniality*, and *recognition cues* (Table 2). These traits are associated with colony structure. Certain traits lead to a competitive advantage for invasive insects; in general, large, unicolonial forms confer invasiveness in social insects by increasing the rates of colony growth and spread (Moller 1996, Tsusui and Suarez 2003). Loss of genetic diversity (Tsusui and Suarez 2003, Suarez et al. 2008, Ugelvig and Cremer 2012) and shifts in colony structure (Wilson et al. 2009) are also related to sustained rapid growth and dispersal of invasive social insects. This is thought to be the case because large supercolonies can be formed from many genetically similar individuals, making the colony more successful. It may be the case that plant coloniality (selfing, reproducing by extensive rhizomes) plays a similar role, although the mechanisms differ.

Foundress activity: Female founders (foundresses) can exemplify different behaviours within the colony. Armstrong and Stamp (2003) found that certain *foundress activity* (higher aggression towards offspring and higher nest repairing tendency) is related to invasiveness in *Polistes dominulus* (European paper wasp) as compared to the native *P. fuscatus* (northern paper wasp). It is unclear whether the aggression of *P. dominulus* foundresses leads to higher colony productivity, but the tendency of *P. dominulus* to be more opportunistic may increase its success as an invasive species (Armstrong and Stamp 2003). Prior to Armstrong and Stamp's (2003) work, it was thought that greater foundress activity would increase foraging behaviour of the workers (Reeve and Gamboa 1987), leading to higher productivity, and thus invasive potential.

Aggression: Aggression is thought to be related to insect invasiveness because it may lead to large, ecologically dominating supercolonies (Suhr et al. 2011). Individuals can display inter- and/or intraspecific aggression, which can lead to differences

in colony structure between native and invasive insects. For ants and termites, invasive species tend to have lower intraspecific aggression than native species (Holway et al. 1998, Suarez et al. 1999, Le Breton et al. 2004, Errard et al. 2005, Cremer et al. 2008, Fournier et al. 2009, Perdereau et al. 2011, Suhr et al. 2011, Ugelvig and Cremer 2012, Hoffmann 2014), suggesting that multiple invasive colonies may behave as a supercolony (Suhr et al. 2011). Interspecific aggression is also exhibited in invasive ants and *Ceratitis catoirii* (Mascarenes fruit fly; Human and Gordon 1999, Cremer et al. 2006, Duyck et al. 2006, Snyder and Evans 2006, Rowles and O'Dowd 2007, Carpintero and Reyes-Lopez 2008, Fournier et al. 2009, Blight et al. 2010, Perdereau et al. 2011). Low intraspecific aggression combined with high interspecific aggression can lead to ecological dominance of the invasive species while allowing individuals of the same species to amalgamate, possibly behaving as a supercolony (Suhr et al. 2011). Aggression may therefore be important in evaluating the potential invasiveness of certain insects and is easily measured between individuals (inter- or intraspecific) using a standard 1-1 assay (Holway et al. 1998).

Queen characteristics: Like *colony characteristics*, this category includes queen traits related to invasiveness: greater *queen number* and greater *queen longevity*. For example, an invasive colony of insects likely contains more queens (Ross et al. 1996, Tsusui and Suarez 2003, Abril et al. 2013), and these queens live longer (Gamboa et al. 2002) than do queens of native species. These invasive characteristics can lead to higher sustained progeny production and thus greater colony growth (Tsusui and Suarez 2003).

Nesting: The habitat used by nesting insects (Suarez et al. 2005, Downing et al. 2012), tendency of the nest to be predated (as a result of mimicry or habitat selection; Cervo et al. 2000), re-nesting after predation (Gamboa et al. 2004), and general nest reuse (Cervo et al. 2000) have all been claimed to be related to insect invasion in different ways. Invasive ants tend to be ground nesters rather than arboreal (Suarez et al. 2005), and invasive wasps tend to nest in urban rather than rural or natural habitats (Downing et al. 2012). Invasive ants and wasps may exploit nest resources not used by their native counterparts (Suarez et al. 2005), leading to their successful establishment. Invasive wasps also tend to encounter less nest predation as a result of their nest location choice (Cervo et al. 2000), and in the case of predation, are more likely to re-nest (Gamboa et al. 2004). Reuse of previous nests is also apparent in invasive wasps, conserving resources and saving time for foundresses (Cervo et al. 2000). These factors lead to a greater probability of establishment, and subsequently invasion, of these species by securing their persistence.

Many of the behavioural traits that are unique to insect invasion are also unique to social insects, which tend to dominate the insect invasion literature (e.g., Holway et al. 2002, Goulson et al. 2003, Kenis et al. 2009, Beggs et al. 2011). Social insects generally possess a suite of traits inherent to their lifestyle that also aids in the invasion process. As discussed above, certain ant species form supercolonies with genetically similar individuals, and these colonies may contain many reproductive females. This state, combined with high aggression, could allow the colony to dominate native species, further amplifying other traits that are important to invasion success, such as reproduction

and development. It is likely that understanding insect social form is critically important in determining the invasive potential of that insect, and therefore must be included in a risk assessment scheme. Because non-social invasive insects tend to be studied less often, there may be other behavioural traits that are important to invasion that are yet to be identified. These traits could be important for the predictive ability of a risk assessment scheme, but would possibly not be comparable to traits found in the AWRA.

Unique invasiveness traits of plants

Just as there are unique traits relating to invasion of insects, mainly relating to social behaviour, there are also a number of traits that are considered to be indicative of weediness in plants that do not generalize to insects. In total, 21 questions in the AWRA are not applicable to insects (Tables 3 and 4). Much of the discrepancy is found in the first four subsections of the AWRA.

Subsection one (three questions) of the AWRA deals with the domestication or cultivation of introduced plants. These questions refer to cases in which plants that have been introduced for horticultural or agricultural purposes, for example, escape cultivation, become naturalized, and then invasive. By contrast, invasive insects have rarely been introduced intentionally, with the exception of biocontrol agents that have become invasive, and so this would not apply to an insect model.

Subsection two (five questions) outlines climate and distribution. *Environmental matching* was identified as important for insect invasion (Table 2); however, the five questions in the AWRA are specific to Australian climatic conditions and should be modified for the specific region of interest (for example, Pheloung et al. 1999 modified the AWRA for use in New Zealand). Also, more *environmental matching* traits relating to abiotic factors were identified for insects than are included in the AWRA. This subsection would likely have to be expanded to apply appropriately to insects.

Subsection three (five questions) contains questions about the weediness of the plant elsewhere. This relates to the notion that success elsewhere can be a predictor of future invasiveness in areas with similar environmental conditions (Panetta and Mitchell 1991). It could also mean that the plant may have an increased probability of escape and spread because it is already naturalized. Whether an insect has been naturalized elsewhere may help to predict future invasiveness as certain species have been found to invade multiple areas (Samways 1999), but this was not identified as important for insect invasiveness in our search of the literature.

Subsection four (12 questions) lists undesirable physical and chemical traits of plants such as whether they produce thorns, spines, burrs, or toxic compounds. Many of these traits do not apply to insects because of their biology. Although it may be possible for an insect to possess mechanical/chemical defenses such as stinging or venom, these are not traits that are currently thought to be important for their invasion success, although they may be related to the ecological impact of the species, and thus would likely not be useful to include in an insect pest risk assessment.

Conclusion

Our systematic review of the invasion literature demonstrates that there are a number of differences in the traits that are claimed to be important for invasion in plants and insects. Species invasion is a complex process that involves both the invading species and its interaction with the biological and physical environment (Hayes and Barry 2008). Using insects as a case study, we have illustrated that expanding a pest risk assessment scheme originally developed for plants (such as the AWRA) may not appropriately capture the potential for invasiveness in other taxa because there are likely to be key differences in both the traits related to invasive behaviour and the importance of these traits. Given that this is the case for insects, it may also be the case for other important invasive taxa such as fish and mammals. Although invasive traits have been identified for plants and validated for a variety of regions (Gordon et al. 2008), consistent correlates of invasion success have yet to be comprehensively assessed across taxa (Hayes and Barry 2008).

Although our analysis identified a number of similar invasion traits for plants and insects, these traits may not carry the same importance in both taxa. For example, we identified many developmental traits that were claimed to be important to the invasion success of insects, while in the AWRA, few questions relate to the development of plants. Whether development, or any other trait, is more predictive of invasion in insects compared to plants would therefore have to be tested.

Furthermore, there are also traits that are unique to plants, as well as traits that are unique to insects. Therefore, the strength and predictive ability of an assessment scheme may be compromised by adapting an assessment for plants to other taxa without comprehensive validation and verification. For example, Coop et al. (2009) were required to further calibrate an invasion screening tool that was adapted from the AWRA to be used on fish. Many of the unique insect invasion-related traits identified were behavioural and were examined in social insects only. Many of these behavioural traits do not transfer directly to plants, but more importantly, non-social insects are largely absent from the insect invasion literature. It is unclear if additional or different traits might also be important to the invasion of non-social insects. The inclusion of behavioural traits may add to the predictive power of an insect risk assessment scheme, and more generally, this highlights a need for further research into invasion-related traits of non-social insects.

A reliable risk assessment scheme must reflect which traits are most strongly indicative of invasiveness for a given taxon. For a rapid risk assessment tool to be useful, consideration must also be given to understanding which traits are easily measured or commonly available in the scientific literature. For example, many of the suggested insect traits (Table 2) may be related to invasiveness but may be difficult to evaluate, especially for insects that are not well studied. The presence of many unanswered questions in any rapid risk assessment tool can compromise its validity and usefulness. Thus, the trade-off between simplicity and accuracy would also require assessment.

Future research development should aim to rate the importance and weight of specific traits related to invasion in taxonomic groups other than plants to develop

comprehensive pest risk assessment tools for other taxa. Currently, we are evaluating which traits are predictive of invasiveness in insects as a first step towards the development of such a tool for insects. Although in this analysis we found that 29 traits are related to invasion in insects, further analysis will inform which of these traits are most important in insect invasion. This approach will consolidate the trade-off between the most indicative and readily available trait information to produce a rapid and efficient design. From this we will know whether differences in invasive traits between taxa require that new risk assessment tools be created for other taxa, or if the approach taken thus far (i.e. making general risk assessments for all non-native taxa) is sufficient.

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